FEEDING, METABOLISM AND GROWTH OF BROWN TROUT

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During a study of the food of brown trout, *Salmo trutta* L. (Elliott 1967, 1970), it soon became apparent that there was an urgent need for basic work on the relationship between feeding and growth before field data could be interpreted successfully. The pioneer studies of Pentelow (1939) and Brown (1946a, b, c, 1951) examined some of the factors affecting growth in trout, but did not attempt to define quantitatively the relationships between these factors. This is the chief purpose of the present study. As the time spent on this project is already equivalent to about twenty-one man-woman years and the work is described in ten papers (Elliott 1972, 1973, 1975a, b, c, d, 1976a, b, c, Elliott & Davison 1975), this short review has to be highly selective.

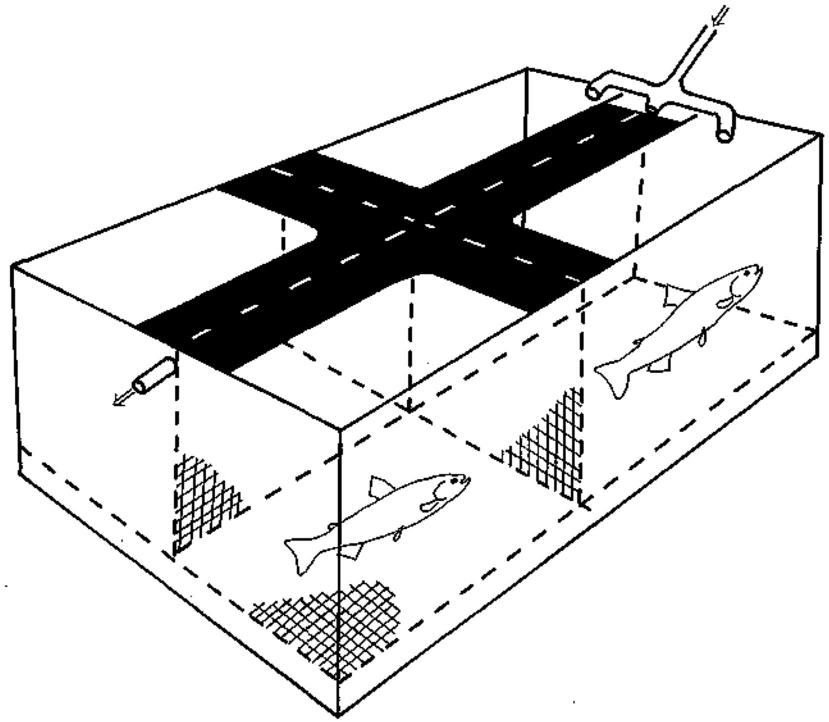

FIG. 1. The general plan of a tank used for the feeding experiments.

Feeding experiments were performed in large tanks (165×90×60 cm) divided into four compartments with one trout in each compartment (Fig. 1). The tanks were partially covered with black polyethylene so that the

fish could retreat to a zone of low light intensity. There was a continuous flow of lake water through the tank and the temperature remained fairly constant. Mean temperatures were similar to those of streams flowing into Windermere, but diel variations in temperature were always larger in the streams. *Gammarus pulex* L. was the food organism in most experiments and was killed just before it was offered to the trout. About 10 cm above the true bottom of the tank was a false bottom of wire mesh through which uneaten food passed and became unavailable to the trout. The total number of food organisms eaten by the trout was converted to energy units by using energy values determined in separate experiments. The methods used to determine the different components of the energy budget are described in detail in the papers.

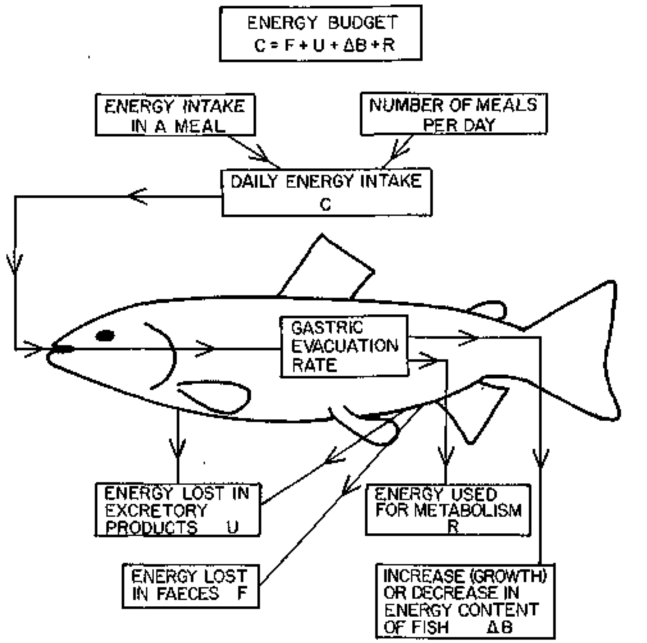

FIG. 2. The relationship between the major components of the energy budget of a trout.

Fig. 2 summarizes the relationships between the major components of the energy budget. The daily energy intake of the trout is the product of the energy intake in a meal and the number of meals in a day. Both the water temperature and the weight of the trout affect the maximum energy intake in a meal, and the relationship between the three variables is well described by a multiple regression equation which can be used to estimate the energy intake of trout of different weights (Fig. 3A). Appetite (measured by voluntary food intake) increases with temperature to a plateau at between 13 and 18°C, and then decreases markedly. The number of meals per day is not significantly affected by the weight of the

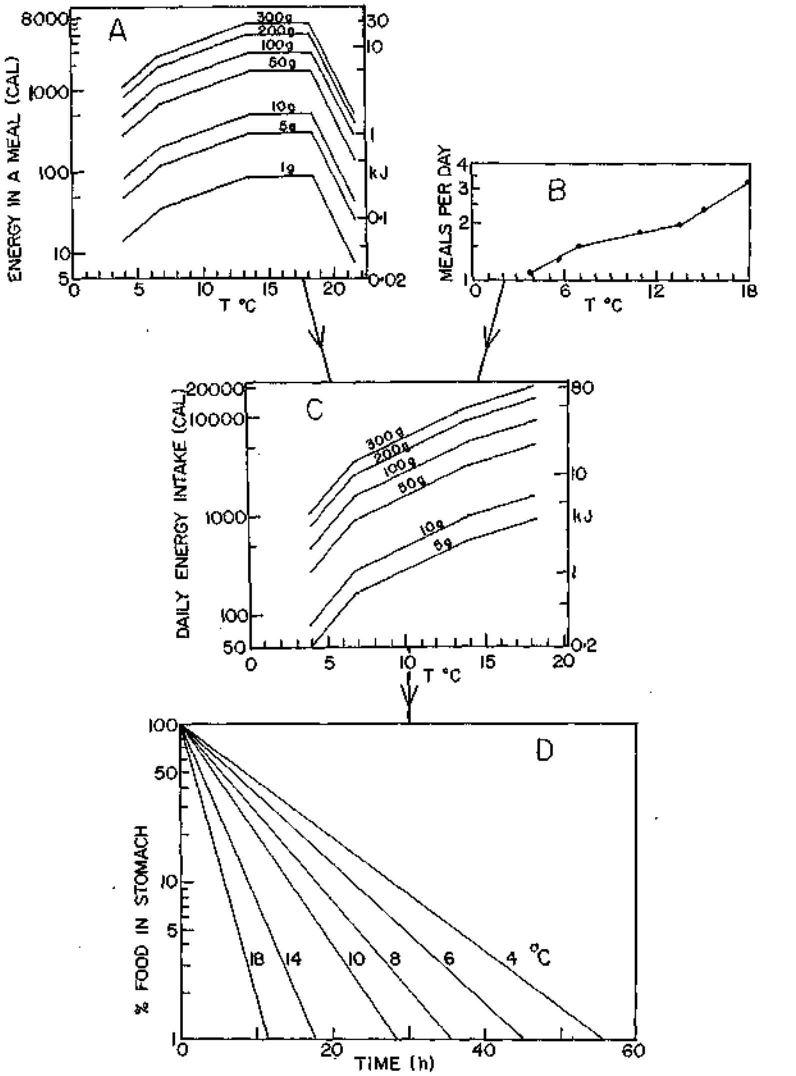

FIG. 3. The relationship between: (A) the maximum energy intake in a meal and water temperature for different live weights of trout; (B) the number of meals in a day and temperature; (C) the maximum energy intake in a day and temperature for different live weights of trout; (D) the percentage of a meal remaining in the stomach and time at different temperatures (note that all ordinates are on log scales).

trout but increases from one meal at about 4°C to three meals at about 18°C (Fig. 3B). As both the energy intake in a meal and the number of meals per day can be estimated, it is also possible to estimate the maximum energy intake per day for trout in the weight range 5–300 g at temperatures between about 4 and 19°C (Fig. 3C). There is a marked decrease in the daily intake at temperatures above about 18°C.

The amount of food in the stomach decreases exponentially with time and the rate of gastric evacuation is related to water temperature (Fig. 3D). Equations have been developed to estimate both the rate and time for the gastric evacuation of different meals at water temperatures between 4 and 19°C. These equations have been found to be applicable not only to brown trout in the laboratory but also to brown and rainbow trout in a Pyrenean stream. Some workers have observed that trout rarely feed at low temperatures whilst others have found trout with full stomachs in the middle of winter. The present study has shown that these observations need not be contradictory. Trout do feed at temperatures as low as 4°C, but there is a long interval between feeding periods because the time required for the gastric evacuation of most of the meal (e.g. 90%) is between one and two days.

The total energy intake of a trout is either lost in the faeces and excretory products or used for metabolism, growth and any reproductive products released by the fish (Fig. 2). Ammonia is the chief excretory product in freshwater teleosts and is excreted primarily from their gills. Smaller quantities of ammonia and urea are the chief excretory products in the urine. These energy losses increase as the weight of the trout increases, but when they are expressed as a proportion of the daily energy intake, the values are not significantly different for different weights of trout. Both temperature and ration size (expressed as a proportion of the maximum energy intake: C/C_{max}) affect the energy losses and thus determine the proportion of the daily energy intake available for metabolism and growth (Fig. 4). The latter increases as ration size decreases, slightly increases with temperature at low temperatures and then slightly decreases with temperature at high temperatures. Winberg (1956) proposed that the average value of the energy available for growth and metabolism in fish is about 80% of the daily energy intake. This value is obviously too high for trout, and a range of 70–75% is more appropriate for most combinations of temperature and ration size.

The energy used in metabolism includes the energy equivalent to that released in the course of metabolism in unfed and resting fish (standard metabolism R_s), the energy required for swimming and other activity (R_a), and the energy required for the processes of digestion, movement and deposition of food materials (R_d). Equations have been developed to estimate total metabolism and standard metabolism, but the other two major components of metabolism could not be separated and have therefore been estimated by difference. Water temperature, energy intake and the weight of the trout are the major variables affecting metabolism.

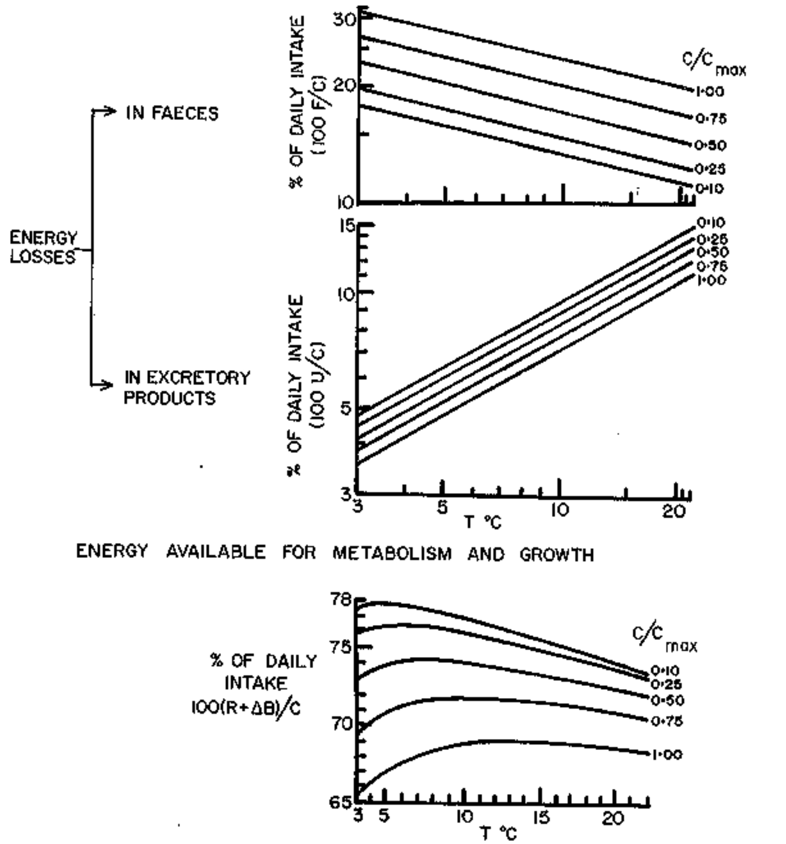

FIG. 4. The relationship between the proportion of the daily energy intake lost in the faeces and excretory products or available for metabolism and growth, and the water temperature at different levels of energy intake (C/C_{max}).

As the weight of the trout and their energy content at the beginning and end of each experiment were known, the total increase (growth) or decrease in the energy content of each fish could be measured. The effect of temperature on the major components of the energy budget of a trout of known weight is shown in Fig. 5. The 'scope for activity' ($R - R_s$) increases markedly with temperature from almost zero at 3·8°C to a maximum at 17·8°C, and then decreases to almost zero at 19·5°C. The energy used for growth (ΔB) increases with temperature to a maximum at 12–13°C and then decreases with increasing temperature. Therefore the equations developed in the present study can be used to estimate the five major components (C, F, U, ΔB, R) and the components of metabolism (R_s, R_{a+d})

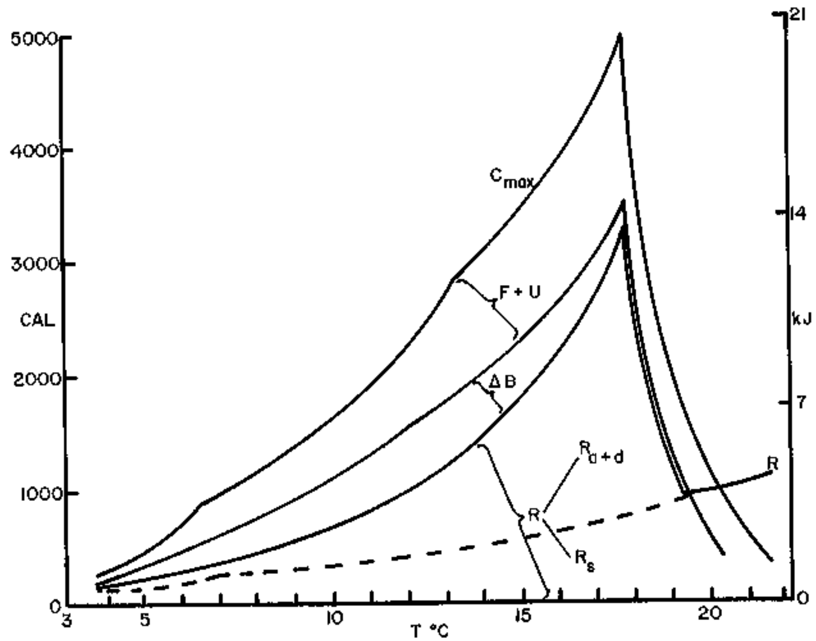

FIG. 5. Division of the major components of the energy budget for trout of 50 g live weight.

for trout in the weight range 10–300 g, in the temperature range 3·8–19·5°C, and on maximum rations.

A general equation for growth with time has been developed, and a second equation describes the relationship between ration size and growth rate expressed as a percentage of maximum growth rate. These equations have been found to be applicable to both wild and hatchery-reared trout feeding on a variety of food organisms in both the stream and the laboratory. They are limited to growth expressed in terms of an increase in the live weight of the trout, and are not suitable for describing changes in the energy content of the fish. It is possible, however, to estimate the maintenance energy intake, i.e. the intake that just maintains a trout without any change in the energy content of the fish ($\Delta B = 0$). The range between the maintenance and maximum energy intakes defines the 'scope for growth', i.e. the range within which the total energy content of the trout increases (ΔB positive). When the energy intake falls below maintenance, the energy content of the trout decreases (ΔB negative). The effect of temperature on the 'scope for growth' for a trout of known weight is shown in Fig. 6. This figure also includes the optimum energy intake, i.e. the energy intake that produces the greatest increase in the energy content of the fish for the least energy intake. The optimum ration is therefore the energy intake at which gross efficiency ($\Delta B/C$) is maximal.

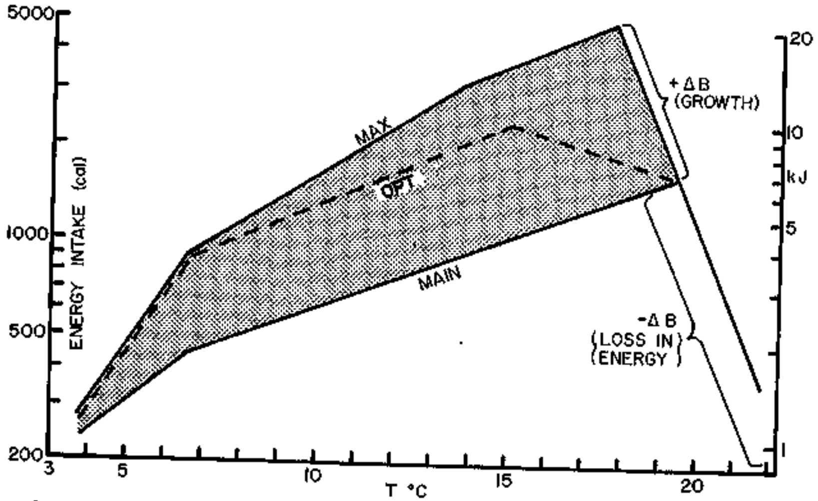

FIG. 6. Relationship between the maximum, optimum and maintenance energy intake for trout of 50 g live weight.

This brief review has dealt with only some aspects of the work and illustrates the complexities of the subject. Although many aspects of feeding and growth in trout have been examined, more work is still required, especially on the components of metabolism, on the energy requirements for reproduction, and on the energy budgets and growth of young trout. The various mathematical models developed in this work have been tested in a few field experiments, but they need to be tested more rigorously before they can be assumed to be adequate.

This work was started at the suggestion of the late F. T. K. Pentelow who provided a lot of encouragement and advice in the early stages of the research. The late F. J. H. Mackereth helped me in the analyses of body composition and excretory products. I wish to thank all those who helped me with the laborious feeding experiments, especially Mrs D. Parr and Mrs D. J. Stephenson for looking after the trout, and Mrs P. A. Tullett for all her assistance in this work.

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